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Running Title: VSTM GAIN FOR SEQUENCED AND REPEATED OBJECTS

**Neural Mechanisms Underlying Visual Short-Term Memory Gain for Temporally
Distinct Objects**

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Abstract

Recent research has shown that visual short-term memory (VSTM) can substantially be improved when the to-be-remembered objects are split in two half-arrays (i.e. sequenced) or the entire array is shown twice (i.e. repeated), rather than presented simultaneously. Here we investigate the hypothesis that sequencing and repeating displays overcomes attentional ‘bottlenecks’ during simultaneous encoding. Using fMRI, we show that sequencing and repeating displays increased brain activation in extrastriate and primary visual areas, relative to simultaneous displays (study 1). Passively viewing identical stimuli did not increase visual activation (study 2), ruling out a physical confound. Importantly, areas of the frontoparietal attention network showed increased activation in repetition but not in sequential trials. This dissociation suggests that repeating a display increases attentional control by allowing attention to be reallocated in a second encoding episode. In contrast, sequencing the array poses fewer demands on control, with competition from non-attended objects being reduced by the half-arrays. This idea was corroborated by a third study in which we found optimal VSTM for sequential displays minimizing attentional demands. Importantly these results provide support within the same experimental paradigm for the role of stimulus-driven and top-down attentional control aspects of biased competition theory in setting constraints on VSTM.

Keywords: Visual short-term memory, working memory, attention, biased competition, fMRI

Multiple objects simultaneously present in the visual field compete for processing resources. An important function of attention is to bias competitive interactions such that neural activity related to non-selected objects is suppressed while activation underlying selected objects is preserved or even enhanced (Desimone and Duncan 1995). Critically, at any given point in time, attentional biasing can only operate on a limited number of items. Tracking tasks with moving stimuli have revealed that the identity of about four independent objects can be maintained simultaneously (Pylyshyn and Storm 1988; Cavanagh and Alvarez 2005), with the capacity of multi-focal attention further decreasing when the number of non-target (distractor) objects is increased (Pylyshyn 2004). Similar limits of attentional capacity are observed during enumeration tasks, with participants able to successfully ‘subitize’ up to 4 numbers (Trick and Pylyshyn 1993). From a theoretical perspective, these limits have been described to reflect the capacity of ‘object individuation’ (Xu and Chun 2009) – a process in which a limited number of objects can be selected based on their spatial position, creating coarse-grained ‘object files’ (Kahneman et al. 1992), which are then elaborated during object identification. Moreover, it has been suggested that limitations of attentional capacity are closely linked to the capacity limits of VSTM (Cavanagh and Alvarez 2005). Evidence for attention as a limiting factor in VSTM capacity has been gathered in brain imaging studies, showing a shared neural substrate, e.g., intraparietal sulcus (Mayer et al. 2007; Mitchell and Cusack 2008), a linear activation increase in these regions with both attentional load (Culham et al. 2001) and VSTM load (Todd and Marois 2004), and an asymptotic activation increase as the memory capacity limit is approached (Linden et al. 2003). Further, individual differences in attentional performance have been shown to underlie differences in VSTM performance (Vogel et al. 2005; Linke et al. 2011). In the present report we explore the novel hypothesis that attentional control – a key construct in the theory of biased competition (Desimone and Duncan 1995) – is a significant factor limiting the capacity of VSTM which can be modulated by temporal distinctiveness of the to-be-encoded stimuli.

VSTM capacity is typically measured with the change detection method in which multiple to-be-remembered items are presented simultaneously in one memory display, followed by a test display containing either the same objects or one new object (Pashler 1988; Luck and Vogel 1997). Using this method, VSTM capacity is estimated to be around 2-4 items only (Cowan 2001). In a previous study, however, we showed that the traditional change-detection approach may underestimate VSTM capacity (Ihssen et al. 2010): Splitting the memory items into two sequential half-arrays dramatically improved VSTM, relative to the canonical (simultaneous presentation) approach. Interestingly, VSTM was also increased when the simultaneous array was presented twice (repeated) rather than being presented continuously for the same duration. In the present studies, in addition to the behavioral approach we used functional brain imaging to investigate how stimulus sequencing and repetition may boost VSTM capacity by overcoming attentional limitations in a manner consistent with the theory of biased competition (Desimone and Duncan 1995).

We hypothesize that in the repetition condition the appearance of a second temporal frame facilitated attentional control. In particular, attention could be disengaged with the offset of the first presentation of the memory displays and reallocated to objects not previously attended with the onset of the display's second presentation, facilitating the encoding and/or maintenance of a larger number of objects. Vogel et al. (2005) found that VSTM capacity was constrained by an individual's ability to filter relevant from irrelevant stimuli. Within the biased competition framework (Desimone and Duncan 1995), such increased attentional control can be interpreted as an enhancement of the top-down biasing of the visual cortex to resolve stimulus competition. In contrast, the sequential condition may increase VSTM by reducing attentional demands in a stimulus-driven manner, since only half of the objects are simultaneously present in the visual field, thereby reducing competition from non-attended items. Under the assumption that not all the objects in an array can be simultaneously attended (Vogel et al. 2005), fewer attentional resources will be necessary to

protect selected items from competing with non-selected items in the sequential relative to the simultaneous condition.

fMRI provides a powerful tool to test the effects of repetition versus sequencing on attention and VSTM: Converging evidence suggests that brain areas associated with object ‘storage’ (e.g., the Lateral Occipital Complex LOC, Xu and Chun 2006) can be disentangled from those associated with attentional control mechanisms, such as regions of the frontoparietal attention network (Corbetta 1998). Accordingly, for both the repetition and sequential conditions we predicted increased activation in visual areas related to object storage, relative to the simultaneous condition. For areas involved in attentional control, however, a divergence between both conditions is expected: While the repetition condition should increase control and lead to increased activation of the attention network, the sequential condition should reduce demands on control and lead to lower frontal activation, as less attention is required to protect the attended items from competition.

Materials and Methods

Paradigm and Study Overview

In Experiment 1, we used a similar change detection paradigm as in our previous study (Ihssen et al. 2010) while acquiring fMRI data. In each trial, participants were asked to maintain a fixed number of briefly shown objects (colored squares and white shapes). Colors and shapes were presented either in two temporally separated displays (*sequential* condition), together in one single display (*simultaneous* condition), or together in a repeated display (*repetition* condition). Participants had to make a (non-speeded) choice response whether a subsequent test display included the ‘same’ objects as shown before (no-change condition), or contained a ‘different’ object (change condition). In the second fMRI study (Experiment 2), we presented the same stimuli but instructed the participants to merely watch the stimulus sequence without any response requirements. The goal of the passive viewing experiment was to rule out the possibility that perceptual differences among the simultaneous, sequential, and

repetition conditions accounted for the differences in the BOLD signal revealed in the memory task of study 1.

Finally, Experiment 3 aimed to further elucidate the neurocognitive mechanisms underlying the VSTM benefit for sequential displays (Ihssen et al. 2010) specifically. In particular, we intended to provide behavioral support for the hypothesis that sequential displays facilitate attention (and increase VSTM) by stimulus-driven decreases in competition arising from non-attended objects. To this end, we used a modified version of our paradigm presenting only the sequential condition but varying the overall number of memory items to be maintained (set size) and importantly the ratio of items in the first versus second sequential display. According to biased competition theory (Desimone and Duncan 1995), items represented in the same receptive field exert mutual suppression, leading to a net decrease in activation. If a stimulus-driven reduction in the number of objects competing for VSTM was crucial for the sequential benefit, optimal performance should arise for ratios distributing the items between the two sequential in a manner that minimizes net competition. As illustrated in Figure 1C, net competition for two sequential displays can be quantified by assigning each possible item pair within a single display one ‘unit’ of competition and then summing these units across the two arrays. With the overall number of to-be-remembered items held constant (e.g. 4), net competition is smaller when the number of items in each display is equal or similar (e.g., 2:2 versus 1:3).

Participants

Participants were university students from Bangor and Cardiff University who had normal or corrected-to-normal vision and gave informed consent to participate in the studies. Sixteen volunteers (15 females and 1 male, age: $M = 24.0$, $SD = 7.9$) participated in Experiment 1. MRI data from additional 10 participants (9 females and 1 male, age: $M = 20.2$, $SD = 1.3$) were collected for Experiment 2, and further 20 volunteers (16 females and 4 males, age: $M = 19.6$, $SD = 4.8$) participated in Experiment 3. All studies had been approved

by the departments' research ethics committees. Participants received monetary compensation or course credits for taking part in the studies.

Materials and Procedure

Experiments 1 and 2. We presented 4 colored squares and 4 white shapes during the encoding phase of each trial (see Figure 1A). Colors/shapes were randomly drawn from a pool of 8 possible objects in each category and presented in groups above (colours) or below (shapes) fixation. In the sequential condition, colors and shapes were presented separately in two different temporal frames, while in the simultaneous and repetition conditions the two subsets appeared together in one single display of 8 objects, presented either once or twice, respectively. Sequential, simultaneous and repetition trials were randomly intermixed.

The rationale for using two stimulus categories (colors and shapes) instead of one category was to give participants in all conditions an equal opportunity to spatially group/chunk memory items. This aimed to reduce the likelihood that a benefit for sequential or repeated displays arose just because items could more easily be spatially grouped when displays were temporally separated. By categorically distinguishing two memory sets, spatial chunking was made possible in in the simultaneous condition as well.

To reduce the likelihood that BOLD responses were contaminated by physical stimulus differences, the simultaneous, sequential, and repetition condition were matched for perceptual load by introducing (task-irrelevant) placeholders which equated the number of objects shown on the screen at a given point in time (see Figure 1A). Accordingly, each trial consisted of two visual events: either two 4-object displays with 4 placeholders in each display (sequential condition), two 8-object displays without placeholders (repetition condition), or one 8-object display and an 'empty' 8-placeholder array (simultaneous condition). Across conditions, the durations of each visual event (full object, half object or empty placeholder display) was matched (350 ms). Equated event durations were important to minimize possible differences between conditions in visual BOLD responses, even though it

led to differences in stimulus presentation time, i.e. the time each individual object was available for encoding. Importantly, our previous study (Ihssen et al., 2010) demonstrated no influence of single object encoding time on VSTM improvement for sequential/repeated displays: Sequential and repeated displays still led to increased VSTM capacity relative to simultaneous displays even when the time the simultaneous display was available for encoding was doubled (700 ms).

----- Figure 1 -----

In the sequential condition, the presentation of colors versus shapes in the first versus second display was balanced across trials and randomly intermixed. In the simultaneous condition, half the trials presented the object array first, the other half presented the placeholder array first, in random order.

In each trial, the two encoding displays were separated by a 950 ms gap, showing a grey fixation cross. After the second encoding display we inserted another 950 ms fixation gap before the test display was shown. The test display showed either 4 colored squares or 4 white shapes with equal probability and in random order, without the participants knowing which subset would be tested. In half of the experimental trials, test displays were identical to the (half-) array shown in the encoding phase (no-change trials). In the other half of the trials, one of the objects shown before was replaced by another (new) object from the same set and in the same location (change trial). Change and no-change trials were randomly intermixed. The test display remained on the screen for 2.4 sec. In Experiment 1, participants were required to respond during test display presentation using a ‘same’ versus ‘different’ button on a response box. No such instruction was given in Experiment 2.

Trials had a total duration of 5 sec (2.6 sec memory display presentation + 2.4 test display) and were separated by a jittered Inter-Trial-Interval of 5 sec (0.5 probability), 7 sec (0.375 probability), or 9 sec (0.125 probability). In Experiment 1 participants performed a total of 192 trials, which were preceded by 20 practice trials outside the MRI scanner. In

Experiment 2 we presented 48 passive viewing trials. Stimuli were presented on a screen behind the MRI scanner, which was viewed through a mirror mounted on the MRI head coil. On the screen, single objects subtended a visual angle of $1.5^\circ \times 1.5^\circ$ (full array: $3.9^\circ \times 9.0^\circ$).

Experiment 3. The same color and shape stimuli as in the fMRI studies were used, presented on a 19" computer monitor and each subtending a visual angle of $1.47^\circ \times 1.47^\circ$, at a viewing distance of 70 cm. Again, objects were presented in groups (colors or shapes) either above or below fixation. No placeholders were presented. Temporal parameters in the change detection task were the same as for the sequential condition in the previous studies, with the exception that trials started self-initiated after participants had responded by pressing the S ('same') or D ('different') key on a computer keyboard. Ratios of items between the first and second memory display were on a continuum, between the same number of items in each display (termed $n : n$) and three more items in one display than the other ($n : n+3$ or $n+3 : n$). Set size was also varied, with the number of stimuli presented across the two displays being either high (7-8 items) or low (4-5 items), as detailed in Table 3. In the colors/shapes half-displays, each object covered one of six possible locations that were rectangularly arranged and filled with objects in a manner identical across ratio conditions. Specifically, we filled the three locations adjacent to the fixation cross first, to avoid gaps in the display; top locations (colours) were filled from right to left, and bottom locations (shapes) from left to right, to minimise instances of more stimuli on one side of the screen than the other.

In half of the trials, the test display probed either the first or second memory display. The test display had the same configuration as the probed memory display, with one of the objects replaced by a new object in half of the trials. We presented 48 trials per ratio condition in random order, resulting in 384 trials in total.

MRI Procedure and Data Acquisition

In Experiment 1, we collected MRI data from 4 functional runs (4 x 48 trials, 4 x 16 trials per condition, 4 x 273 volumes) and one structural run, resulting in a total scanning time

of approximately 40 minutes. In Experiment 2, data were acquired in one functional run (48 trials, 16 trials per condition, 273 volumes) that was performed after participants had completed a different, unrelated imaging study ($N = 10$) or after scanning in Experiment 1 ($N = 3$). MRI images were recorded with a Philips 3T scanner equipped with a SENSE parallel head coil. BOLD signals during the VSTM task were acquired with a gradient echo planar T2*-weighted sequence, synchronized to the onset of experimental trials and covering most of the cerebrum (TR = 2,000 ms; TE = 35 ms; matrix size = 96 x 96; FOV = 220 x 220 mm²; voxel size = 2.3 x 2.3 x 3 mm³; flip angle = 90°; number of slices = 30 contiguous axial slices). After half of the functional runs, structural images were acquired with a high-resolution T1-weighted volume scan (voxel resolution: 1 mm³).

Behavioral Data Analysis

VSTM capacity for each condition was estimated using the formula proposed by Pashler (1988): $k = (\text{hit rate} - \text{false alarm rate}) / (1 - \text{false alarm rate}) * \text{set size}$. In comparison to the widely used formula proposed by Cowan (2001), Pashler's k is more appropriate when the probe display contains more than a single item (Rouder et al. 2011). To obtain a different measure of VSTM performance that is independent from the theoretical assumptions underlying the k formulae (e.g. discrete slots), we also calculated d' sensitivity scores in Experiment 1 (which had a fixed set size), with $d' = Z(\text{hit rate}) - Z(\text{false alarm rate})$.

Experiment 1: Participants' k and d' values in each condition entered separate repeated-measurement Analyses of Variance (ANOVA) using *Presentation Mode* (3; simultaneous, sequential, repetition) as a within-subject factor. Significant effects were followed by paired t-tests (significance level: $p < 0.0167$ [Bonferroni-corrected]).

Experiment 3: To control for the effects of decay and recency, k values were averaged over display order (e.g., 1:3 and 3:1 were averaged) to produce a single estimate for each ratio. We then calculated average k values for low (4-5 items) versus high (7-8 items) set sizes, presented in near ($n : n$, $n : n+1$, $n+1 : n$) versus far ($n : n+2$, $n+2 : n$, $n : n+3$, $n+3 : n$)

ratios, which were then submitted to two-factorial repeated measurement ANOVA (set size [low, high] x ratio [near, far]).

MRI Data Preprocessing and Data Analysis

Using the BrainVoyager QX software, we submitted functional raw images to canonical artefact correction algorithms (slice scan time correction, 3D motion correction using trilinear interpolation, and a 0.006 Hz temporal high pass filter) and then realigned and coregistered them with participants' anatomical scans. Functional images were interpolated to iso-voxels ($3 \times 3 \times 3 \text{ mm}^3$) spatially normalized by transforming them to Talairach space ($1 \times 1 \times 1 \text{ mm}^3$). We further preprocessed the resulting volume time courses using spatial (4 mm) and temporal (2.8 sec) Gaussian smoothing. Z-transformed volume time courses were analyzed using a whole-brain General Linear Model (GLM) with 3 regressors that corresponded to the three conditions and were convolved with a canonical hemodynamic response function locked to the onset of each trial and modeling BOLD activation across the whole 5 sec of each trial. The resulting beta values were submitted to a second-level random effect analysis of variance (ANOVA and tested with three contrasts: Sequential - simultaneous (seq - sim), repetition - simultaneous (rep - sim) and repetition - sequential (rep - seq). Initial statistical t-maps were created at a p -level of $p < 0.01$, which was adjusted to $p < 0.005$ for the rep - sim and to $p < 0.001$ for the rep - seq contrast. To control for multiple comparisons in whole-brain analyses, we used the cluster-level statistical thresholding tool implemented in Brainvoyager which for each of the three volumetric statistical maps calculated through Monte-Carlo simulations (1000 iterations) a cluster size threshold corresponding to a corrected p -level of $p < 0.05$ which we further bonferroni-corrected to $p < 0.0167$, taking into account that three different contrasts were computed. Map-specific corrections resulted in a minimum cluster size of 378 voxels (in transformed $1 \times 1 \times 1 \text{ mm}$ Talairach space) for the seq - sim contrast, 405 voxels for the rep - sim contrast and 243 voxels for the rep - seq contrast.

Whole-brain GLM analysis of functional MRI data of Experiment 2 was similar the procedure of Experiment 1 and aimed to examine whether passively monitored sequential/repeated displays elicited a similar BOLD effects observed in the first study during the VSTM task. Based on the results of Experiment 1, we specifically examined (i) whether sequential displays elicited larger activation than simultaneous displays in any visual area (seq > sim) and (ii) whether the repetition condition was related to increased activation in visual regions as well as in areas of the frontoparietal attention network, relative to the simultaneous condition (rep > sim). To determine significant clusters, we again used an uncorrected p -level of $p < 0.01$ but – due to the lower statistical power of Experiment 2 consisting of one functional run only (48 trials) – then used a low cluster-level threshold of 5 fMRI (3 x 3 x 3 mm) voxels corresponding to 135 voxels in analysis space (1 x 1 x 1 mm).

In addition to the whole-brain contrasts, we carried out an ROI analysis in which we compared beta values extracted for the three different conditions under passive viewing instructions in those clusters that we had identified in the contrast analysis of Experiment 1. Differences between the three conditions were tested using paired t -tests (significance level: $p < 0.05$).

fMRI Connectivity Analysis (Psychophysiological Interaction PPI; Experiment 1)

As delineated above, we predicted a divergence between the sequential and repetition condition with regard to the engagement of attentional control regions. Specifically, we hypothesized that for the repetition condition frontal and parietal regions more strongly mediate the increases of brain activation in visual brain areas (e.g., LOC), reflecting increased top-down resolution of stimulus competition. Conversely, such top-down influences should be less pronounced for sequential half-arrays which entail a stimulus-driven reduction of stimulus competition. One approach to examine such modulations that reveal effects specific to an experimental task condition is the PPI method.

Briefly, the PPI method tests for a change in the contribution of one area to a second area that is contingent on a specific experimental manipulation (Friston et al. 1997).

Technically, the PPI approach aims to identify brain regions which show *task- or condition-related correlations* with a chosen seed region, i.e., whose BOLD signal time courses can be explained by the interaction between a physiological factor (time course of seed region) and a psychological factor (task contrast/regressor). Here we used as seed regions frontal and parietal areas showing an overall sensitivity towards temporal variations of the memory display, i.e. a main effect of *Presentation Mode* (3; simultaneous, sequential, repetition) in a Random Effects GLM. In this way, we obviated any bias towards either the repetition or sequential condition arising when clusters identified in the simple contrasts analysis were used as seed regions. Frontal seed regions produced by the main effect GLM included two regions straddling the left and right inferior frontal sulcus (IFS), clusters located in the left DLPFC and right PMC as well as a cluster in the right pre-supplementary motor areas (pre-SMA; see Table 2 for seed region details). In addition, the main effect GLM identified seed regions in the left and right IPS, leading to 7 seed regions and thus 7 separate PPI analyses all together.

The PPI term was calculated as the element-wise product of the mean time course in the seed region (physiological factor) and a hemodynamic response function vector reflecting larger activation in the repetition versus sequential condition (= difference repetition-sequential = psychological factor). Beta values were extracted by estimating a whole-brain fixed effect model with 3 regressors (physiological, psychological, and PPI factor) first, which were then entered in a second-level random effect analysis with two regressors (PPI, baseline). Regions showing a significant effect of the PPI regressor were identified using an initial uncorrected p -level of $p < 0.005$ and cluster-level thresholding with a corrected p -level of $p < 0.05$ that we further bonferroni-corrected to $p < 0.007$, given that 7 PPI analyses were conducted for the 7 seed regions. Calculated map-specific minimum cluster sizes for the 7

contrasts ranged from 10 to 14 fMRI voxels, corresponding to 270 to 378 voxels in Talairach space.

Results

Experiment 1

Behavioral results

ANOVA on k scores showed a significant main effect of *Presentation Mode*, $F(2, 30) = 10.30, p < 0.001$, reflecting increased VSTM capacity estimates for both the sequential, $t(15) = 5.56, p < 0.001$, and the repetition condition, $t(15) = 3.46, p = 0.0035$, relative to the simultaneous condition (Figure 1B). There was no significant difference between performance with sequential versus repeated displays, $t(15) = 0.42, p = 0.678$. We obtained an identical pattern of results for d' scores, showing a strong effect of *Presentation Mode*, $F(2, 30) = 8.90, p < 0.001$, which was caused by performance increases in the sequential ($M = 1.34, SE = 0.14$), $t(15) = 5.25, p < 0.001$, and repetition condition ($M = 1.45, SE = 0.17$), $t(15) = 3.53, p < 0.01$, relative to the simultaneous condition ($M = 0.85, SE = 0.09$). Again, there was no significant difference between the sequential and repetition condition, $t(15) = 0.62, p = 0.545$.

FMRI Results

Seq - sim: We found 3 clusters showing increased activation for sequential versus simultaneous displays (see Table 1 for cluster sizes and coordinates): In accord with our hypotheses, the sequential condition was associated with increased BOLD responses in visual regions, showing significant effects in both extrastriate (Lateral Occipital Complex/LOC) as well as in primary visual areas (V1, see Figure 2), but with similar responses (i.e. no significant differences) in the frontoparietal attentional control network, relative to the simultaneous condition. The sequential condition also elicited stronger BOLD responses than the simultaneous conditions in the right striatum. We did not find any region that showed reduced BOLD responses in the sequential relative to the simultaneous condition.

----- Table 1 -----

Rep - sim: Consistent with our hypotheses, we observed a different pattern for the contrast between the repetition and simultaneous condition: Repeated displays evoked stronger BOLD responses in several parietal and frontal regions, including the left and right intraparietal sulcus (IPS) as well as the right dorsolateral prefrontal cortex (DLPFC, see Table 1), i.e. areas that play a key role in the frontoparietal attention network (Corbetta et al. 1998). Similar to the sequential condition, we also observed an increase in extrastriate visual activation, showing significant effects in the right LOC and in a cluster within the right inferior occipital gyrus (IOG). Finally, the repetition condition was related to heightened responses in the right (ventral) striatum and a region in the right anterior insula. Again, the whole-brain contrasts revealed no significant regions showing a reversed pattern, i.e reduced activation for repeated relative to simultaneous displays.

Rep - seq: Consistent with the idea of a greater engagement of the (right) frontoparietal attention network, three clusters showed larger activation in the repetition relative to the sequential condition (see Table 1): Right IPS, right DLPFC and an area in the right premotor cortex (PMC). Importantly, we did not observe any differences between the repetition and sequential condition in early or higher-order visual areas, such as those identified for the seq - sim and rep - sim contrasts. Together, these findings suggest that repeated and sequential displays both increased activation of visual areas during the VSTM tasks, with the peaks of visual activation showing some variation though (sequential condition: primary visual cortex and left LOC, repetition condition: right IOG and right LOC).

----- Figure 2 -----

PPI Analysis

To further examine the divergence between the sequential and repetition condition with regard to the engagement of attentional control regions, we analyzed connectivity (PPI)

between brain regions. Specifically, we hypothesized that for the repetition condition frontal and parietal regions more strongly mediate the increased activity observed in visual brain areas, reflecting increased top-down influence when attention can be reallocated to different (previously not attended) objects with the occurrence of the second (repeated) display. Conversely, such top-down influences should be less pronounced for sequential half-arrays, which diminish attentional demands by entailing a stimulus-driven reduction of stimulus competition (see Figure 1C).

----- Figure 3 -----

Overall, we found 20 clusters that showed higher connectivity with one of the 7 seed regions in the repetition versus sequential condition, including prefrontal, pre- and postcentral clusters in the vicinity of the seed region or in the contralateral hemisphere as well as several cerebellar clusters. Importantly, 9 of the clusters showing condition-specific connectivity with one of the seed regions were located in the extended visual cortex (see Table 2). Connectivity with visual regions was predominantly intrahemispheric and particularly extensive between bilateral IPS and the ventral visual cortex. These findings suggest that the frontoparietal network indeed exerted a stronger top-down influence in the repetition condition relative to the sequential condition, leading to a boost of storage-related visual activation (which in the sequential condition was elicited by the stimuli themselves).

----- Table 2 -----

Experiment 2

Passively viewing sequential displays did not lead to increased activation relative to simultaneous displays in any region of the brain ($\text{seq} > \text{sim}$). For the $\text{rep} > \text{sim}$ contrast, we found only one region on the right lateral parietal surface (supramarginal gyrus, mean coordinates: $x = 55$, $y = -32$, $z = 19$, cluster size: 140 voxels) showing significant effects. Further, when beta values extracted from passive viewing trials were submitted to a ROI analysis using the clusters identified in Experiment 1, t-tests showed that neither in clusters

identified by the seq - sim contrast of Experiment 1 nor in clusters identified by the rep - sim contrast of Experiment 1 passive viewing elicited any significant effects (seq - sim: all $ps > 0.12$; rep - sim, all $ps > 0.18$). The only trend-level effect we found was a *decrease* of activation for passively viewed sequential relative to passively viewed simultaneous displays in the right striatum ROI ($p = 0.083$). Importantly, these effects were in opposite direction compared to Experiment 1.

Experiment 3

When the number of presented objects and their distribution across the two sequential displays were varied (Experiment 3, see Figure 1C), ANOVA on k values showed a significant main effect of ratio, $F(1,19) = 5.99$, $p = 0.024$, but neither a main effect of set size, $F(1,19) = 0.47$, $p = 0.501$, nor an interaction ratio x set size, $F(1,19) = 0.02$, $p = 0.880$. Consistent with our hypotheses, the main effect of ratio reflected increased VSTM capacity with sequential displays when items were split in near (mean k : 3.24) versus far (mean k : 2.76) ratios. In other words, VSTM was improved when the items were divided into the two sequential displays in a way that reduced the overall number of within-display suppressive interactions.

----- Table 3 -----

Discussion

In the present study we find increased VSTM capacity for sequential and repeated object arrays, relative to the simultaneous presentation of the same objects, replicating our previous results (Ihssen et al. 2010). Going further, using functional imaging, we distinguish separate neural processes that underlie each of the two increased memory performance conditions. Importantly, this provides evidence within the same experimental paradigm for stimulus-driven and top-down mechanisms by which attentional limitations constrain VSTM capacity. Moreover, our findings may provide both basic and applied researchers with

information vital to the design and use of strategies for effective deployment of visual short-term memory.

The present fMRI results reveal that presenting two temporally segregated displays is associated with an increase in both VSTM capacity and visual cortex activation. Consistent with our hypotheses, both the repetition and sequential conditions elicited BOLD signal increases in extrastriate visual areas, such as the LOC and IOG, relative to the simultaneous condition. We did observe some divergence between the seq - sim and rep - sim contrasts with regard to which specific regions showed significant effects. However, we did not find any significant difference in visual activation between the two conditions themselves (rep - seq contrast) and thus interpret the regional divergence observed between the seq - sim and rep - sim effects as a result of normal variability as to the exact parts of the visual network that are recruited. Even if both conditions (sequential and repetition) rely on visual cortical resources they do not necessarily need to recruit exactly the same areas, since there is degeneracy and redundancy in any cortical system (Friston and Price 2003). Following previous brain imaging work (Xu and Chun 2006; Sligte et al. 2009), the observed boost in activation in extrastriate visual areas most likely reflects the ‘contents’ of VSTM, which in our study encompassed a larger number of correctly recalled items in these two conditions. Specifically, the role of LOC has been described as storing a variable number of objects, differentiating it from parietal regions involved in the deployment of attention (Xu and Chun 2006). Other studies have emphasized the importance of ventral occipitotemporal visual areas for VSTM, for example, V4 (Sligte et al. 2009) or the anterior fusiform gyrus (Courtney et al. 1997). These results corroborate our finding of activation increases in IOG in the repetition condition.

Recently, VSTM has also been linked to early visual areas, e.g., V1, suggesting that maintenance of visual information during delay is accomplished by sustained activity in the same regions that are active during encoding (Pasternak and Greenlee 2005; Ester et al. 2009;

Serences et al. 2009). Moreover, multivoxel pattern classification approaches suggest that contents of VSTM can be decoded from activation in (striate and extrastriate) visual areas but not from BOLD responses in IPS and frontal areas (Linden et al. 2012; Riggall and Postle 2012; Emrich et al. 2013). Together, these findings indicate that increased visual activation as observed in sequential and repetition trials reflects VSTM-related activation. With regard to the sequential condition, future work will need to establish to what extent the functionally specific increase in visual activation is accomplished by bottom-up (sensory) mechanisms of competition resolution during encoding of sequential stimuli (Kastner et al. 2001; Emrich and Ferber 2012), and/or top-down, recurrent control from higher-order areas in response to specific task demands.

Our results go beyond a mere corroboration of the contribution of visual areas to VSTM because they reveal the interplay between visual areas and the frontoparietal network in modulating VSTM capacity. In particular, the observed increase of IPS activation in the repetition relative to the simultaneous condition can be viewed as a consequence of increased attentional deployment (Corbetta and Shulman 2002) and/or as a consequence of the higher number of VSTM items stored, i.e. VSTM load (Todd and Marois 2004). Both effects can be attributed to increased attentional control in the repetition condition (see below). The notion that VSTM can be improved simply by allowing two rather than one encoding epochs, even when single object encoding time is equated (Ihssen et al. 2010), corroborates a model by Bowman and Wyble (2007) according to which episodic segmentation or distinctiveness improves the encoding and/or maintenance of visual information.

The question arises why we didn't observe any increased IPS activation for sequential versus simultaneous trials. As delineated above, the IPS has been implicated in both attentional and VSTM functions and its specific role in these functions is still subject to debate. While the lack of IPS activation increase in sequential trials is consistent with the attentional interpretation (see below), it conflicts with the notion of IPS responses reflecting

VSTM load (which was higher in the sequential condition). However, pertinent to the present findings IPS activation has been linked to the recalibration of an ‘attentional priority map’ (Molenberghs et al. 2007). According to this model, the occurrence of a second memory display (either in the sequential or repetition condition) may evoke a redistribution of attentional weights in order to resolve stimulus competition. In the repetition condition, on occasion of the second display weights are reassigned from objects that have been encoded during exposure to the first repetition display to items that have not yet been encoded. Critically, this attentional recalibration depends on a subtle distinction between encoded and not yet encoded objects. In contrast, in the sequential condition, attentional recalibration is facilitated by the distinctiveness between placeholders and to-be-encoded objects and the predictability of their spatial location in the second display based on the location of the first half-array. This difference in the difficulty of attentional recalibration (high in the repetition and low in the sequential condition) may account for the observed increase in IPS activation for the repetition relative to the sequential condition. The importance of encoding factors on IPS activation during change detection tasks has been highlighted in a study by Gillebert et al. (2012) showing that IPS responses vary as a function of both the number of targets and the number of distractors

Repetition trials were also accompanied by increased activation in frontal regions, relative to both simultaneous and sequential trials. Consistent with our hypotheses, BOLD response amplification occurred most prominently in areas that constitute key nodes of the attentional control network (right DLPFC, right PMC; Corbetta and Shulman 2002; Simon et al. 2002). We suggest that in the repetition condition the second appearance of the 8-item-display facilitated attentional control, allowing participants to redistribute attentional weights (see above); in turn leading to higher activation of control-related neural circuits. In contrast, splitting the memory display into two half-arrays in the sequential condition did not evoke stronger engagement of frontal control areas, relative to the simultaneous. Consistent with our

hypotheses, sequencing to-be-remembered items thus decreased demands on attentional control, as reflected in activation of the frontoparietal network. Our psychological explanation would be that object segmentation was achieved by the successive displays themselves. In other words, objects were more easily selected and better protected from competition from non-attended items in half- compared to full object arrays. This interpretation is in accord with a study by Scalf and Beck (2010) who showed that the amount of competition at the level of stimulus representation determines how efficiently objects can be selected (i.e., attended): When five Gabor stimuli were presented either sequentially or simultaneously (Experiment 1), only the sequential presentation allowed for successful attention to multiple items, as shown by preserved BOLD activation in V4, relative to attending to a single item.

Further evidence for a facilitatory effect of sequencing on attention (and thus VSTM capacity) was provided by Experiment 3: When varying the ratio of items presented in the first versus second sequential display, we observed improved performance for ratios in which the number of mutual suppressive interactions between objects was reduced or, in other words, competitive demands on attentional control were minimized. These results are consistent with a recent study showing that when dual-feature objects consisting of colors at specific locations are presented sequentially rather than simultaneously, the number of binding errors at subsequent recall is reduced (Emrich and Ferber 2012). The authors attributed these effects to a reduction of item competition at early sensory encoding stages.

Even though our results support the *general* notion of competition resolution underlying sequential memory benefits as well, the present effects cannot be *fully* explained by a reduction of sensory (bottom-up) competition as in the study by Emrich and Ferber. One argument against a purely sensory explanation is that we did not find increased visual responses in sequential trials in the passive viewing study similar to those reported by Kastner et al. (2001). The present sequential effects thus appear to be driven by an interplay between a

sensory (bottom-up) reduction of stimulus competition and top-down control further enhancing the resolution of competition.

Finally, the results of the PPI analysis support the conclusion that the repetition and sequential VSTM benefits are dissociable with regard to the neural mechanisms involved: Modulation of ventral visual cortex activity by frontoparietal regions was stronger in the repetition than in the sequential condition, indicating that in the former, control regions exerted a stronger (top-down) influence on regions associated with VSTM storage. Consistent with our finding of increased frontoparietal-occipital connectivity in the repetition condition, enhanced coupling between prefrontal and extrastriate visual areas – indexed by increased phase synchronization of theta frequencies – was recently shown to predict visual short-term memory performance in monkeys (Liebe et al. 2012).

To summarize, our results reveal that sequencing and repeating visual memoranda leads to similar effects in occipital and inferior temporal regions that are implicated in short-term *storage* but to dissociable responses in inferior parietal areas associated with redistributing *attentional weights*, and frontal regions responsible for *controlling* attention. Importantly, the present results corroborate recent views on the contribution by and dynamic interaction of multiple brain areas to the construct known as visual short-term memory.

Possible alternative accounts and related findings

In our previous behavioral study (Ihssen et al. 2010) we ruled out several mechanisms that cannot account for the sequential and repetition VSTM benefits, such as facilitated encoding of configural information, differences in encoding time (see also Methods), and strategic encoding of the first sequential display at the expense of the second. The question arises of whether the present neural activation patterns can be accounted for by alternative mechanisms: One might argue that the observed increase of visual activation in the sequential and repetition conditions was driven by physical stimulus differences during encoding alone. Specifically, the appearance of two displays, which both contained objects, may be

qualitatively different than two displays showing objects in one and only placeholders in the other display (simultaneous condition). Results from Experiment 2 provide clear evidence against this competing account: Passively viewing sequential or repetition displays did not increase visual BOLD responses relative to simultaneous displays.

At first glance the passive viewing results seem to conflict with the BOLD signal increase in visual areas reported by Kastner et al. (2001) for (non-attended) sequential relative to simultaneous displays. The authors interpreted the amplifying effect of temporal separation on visual activation as reflecting a sensory, bottom-up reduction of stimulus competition (cf. Beck and Kastner 2009). As delineated above, we believe that such early and sensory mechanisms of competition reduction cannot be the *only* source of to the sequential benefit in our paradigm, since sequential displays did not produce increased visual responses during passive viewing. One reason for the lack of visual effects is that we presented placeholders to equate low-level perceptual load among conditions, which is likely to have mitigated differences in early, sensory competition. Accordingly, while in Kastner et al. (2001) the increase of visual activation for sequential displays may have occurred in a purely passive, feed-forward manner, increased visual activation in our sequential VSTM task appears to originate at least partly from active, goal-directed processing (i.e., attention). Whereas the contribution of pure feed-forward, bottom-up mechanisms, e.g., lateral inhibition, has yet to be further examined, the present results reveal the importance of stimulus-driven effects on attention for their contribution to VSTM capacity.

Effects of repeating items as examined here have also been the focus of the ‘preview task’ in which a visual search array partly repeats distractor items that have been presented in a preceding preview array (Watson and Humphreys 1997; Olivers et al. 2005). Consistent with the beneficial effects of repetition on VSTM, repeating distractors in visual search facilitates performance. Similar to the mechanisms underlying repetition benefits that we propose here, preview facilitation has been explained by enhanced top-down attentional

control and is accompanied by increased parietal activation in attention-related areas (Olivers *et al.* 2005). In both tasks, repetition may thus act to prioritize new items. However, while in the preview task this allows observers to ignore previously presented items, repetition in our task enables observers to redistribute attentional weights to new targets even though the previously selected objects have to be maintained in VSTM.

Conclusions

The present results explain at the neural level a new behavioral phenomenon – VSTM improvement by temporal stimulus separation – which has implications for learning theory and practice. For instance, temporal segregation of the stimulus input may provide an avenue to train working memory capacity in clinical conditions that are associated with impairments in this domain, such as schizophrenia, learning disabilities, or neurodegenerative diseases. Our data suggest that VSTM capacity is constrained by attentional limitations during encoding of the to-be-remembered objects and that temporal separation of the presented objects can act to overcome these constraints, thereby increasing VSTM capacity. Moreover, we reveal in the same experiment a functional dissociation between the facilitatory mechanisms of display repetition versus display sequencing at both the psychological and the brain circuit level. In the sequential condition a stimulus-driven facilitation of VSTM was accomplished by displays in which competition between attended and non-attended items is reduced. At the neural level, this was reflected in higher activation of visual areas and lower activation of frontoparietal areas. In the repetition condition display repetition facilitated attention (and VSTM) by increased top-down control exerted by frontal areas over visual areas. This was reflected in activation increases in both visual and frontoparietal areas. Importantly, the present results reveal the dynamics of the brain as it instantiates visual working memory in response to changing task conditions.

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Table 1. Anatomical details of significant clusters in Experiment 1.

	Region (L/R)	Center of gravity (x, y, z)	Peak voxel (x, y, z)	Cluster size (voxel)
Seq - sim	LOC (L)	-29, -80, 5	-31, -80, 3	412
	Striatum (R)	16, 8, -5	14, 7, -6	672
	V1 (L/R)	5, -73, 0	17, -65, 3	1356
Rep - sim	DLPFC (R)	37, 26, 22	38, 22, 24	928
	Insula (R)	28, 15, 9	29, 16, 9	452
	IPS (L)	-32, -60, 39	-31, -59, 39	2948
	IPS (R)	24, -66, 33	32, -62, 27	3658
	IOG (R)	35, -68, -14	35, -62, -18	964
	LOC (R)	28, -73, 14	26, -77, 15	1714
Rep - seq	DLPFC (R)	39, 23, 27	38, 25, 33	1693
	IPS anterior (R)	40, -46, 34	35, -47, 30	2091
	IPS posterior (R)	28, -64, 31	29, -62, 30	2439
	IPS (L)	-27, -57, 32	-28, -56, 33	320
	PMC (R)	37, 0, 29	35, -2, 33	643

Note: The table shows Talairach coordinates of centers of gravity (= mean coordinates), coordinates of the voxel showing highest statistical significance and the size (in $1 \times 1 \times 1 \text{ mm}^3$ voxel) of clusters identified by whole-brain contrasts between the sequential (seq), repetition (rep) and simultaneous (sim) conditions. Note: Initially, the right IPS and right LOC clusters in the rep - sim contrast included overlapping voxels but were split based on functional and anatomical consideration using a horizontal parting plane which separated the superior ($z > 23$, IPS) and inferior (LOC, $z < 23$) cluster parts.

LOC = Lateral Occipital Complex, DLPFC = Dorsolateral Prefrontal Cortex IPS =

Intraparietal Sulcus, IOG = Inferior Occipital Gyrus, PMC = Premotor Cortex.

Table 2. Results of the Psychophysiological Interaction (PPI) analysis of Experiment 1.

Frontal or parietal seed region (L/R)	Visual cluster showing larger connectivity to seed region in repetition versus sequential condition	Center of gravity of connected cluster (x, y, z)	Size of connected cluster (voxels)
Center of gravity (x, y, z) Size (voxels)			
IPS (L) -32, -58, 39 3046	Calcarine Sulcus (L/R) Lingual Gyrus (L) Lateral Occipitotemporal Gyrus (L) Inferior Occipital Gyrus (L)	3, -75, -1 -23, -73, -16 -30, -56, -16 -38, -74, -11	1566 337 294 337
IPS (R) 30, -59, 35 7139	Lateral Occipitotemporal Gyrus (R) Medial Occipitotemporal Gyrus (R)	35, -58, -12 33, -31, -20	780 658
IFS (L) -38, 24, 21 289	—		
IFS (R) 34, 20, 18 6904	Medial Occipitotemporal Gyrus (R)	29, -34, -21	361
PMC (R) 39, -1, 33 4649	Medial Occipitotemporal Gyrus (R)	28, -32, -21	602
DLPFC (L) -44, 18, 32 270	Lateral Occipitotemporal Gyrus (L)	-32, -66, -13	623
Pre-SMA (R)			

5, 13, 45

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879

Note: The table lists anatomical details (Talairach mean coordinates and cluster sizes) of clusters showing increased connectivity (= main effect of PPI regressor) to frontoparietal seed regions in the repetition relative to the sequential condition. Seed regions were identified in a Random Effects GLM analysis as clusters showing a main effect of *Presentation Mode*.

IPS = Intraparietal Sulcus, IFS = Inferior Frontal Sulcus, PMC = Premotor Cortex, DLPFC = Dorsolateral Prefrontal Cortex, pre-SMA = Presupplementary Motor Cortex.

Table 3. Experimental conditions in Experiment 3.

	n : n	n : n+1 or n+1 : n	n : n+2 or n+2 : n	n : n+3 or n+3 : n
Low set size (4, 5)	2 : 2	2 : 3 or 3 : 2	1 : 3 or 3 : 1	1 : 4 or 4 : 1
High set size (7, 8)	4 : 4	3 : 4 or 4 : 3	3 : 5 or 5 : 3	2 : 5 or 5 : 2

Note: The table illustrates how set size and item ratio in sequential displays were manipulated in Experiment 3. No simultaneous or repetition displays were used in this study as VSTM performance was predicted to vary within the sequential condition, showing increasing VSTM for equal or near versus far ratios.

Figure Captions

Figure 1. (A) Stimulus examples (color stimuli shown in greyscale) and trial timing for the three experimental conditions in the VSTM change detection task of Experiment 1. (B) Behavioral results of Experiment 1: Estimates of VSTM performance using Pashler's k for simultaneous (sim), sequential (seq), and repeated (rep) displays. Error bars indicate the standard error of the mean. (C) Experimental rationale of Experiment 3: Example of how different ways (= ratios) of presenting 4 items in the two sequential displays used in Experiment 3 determines the degree of object competition (and thus attentional demands). Each arrow represents one 'unit' of competition, so this hypothetical example reduces competition from 12 units with all items presented together (left panel), to 6 units with 3 items in one display and 1 in the other (middle panel), and to 4 units with 2 items per display (right panel).

Figure 2. Results of the whole-brain BOLD signal contrast analysis of Experiment 1. Statistical maps show positive t -values larger than the statistical threshold in orange for the three different contrasts (sequential versus simultaneous, repetition versus simultaneous and repetition versus sequential). Maps were corrected with cluster-level thresholding at $p < 0.0167$ and are overlaid on a Talairach-transformed structural MRI image of a representative participant. Crosshair lines indicate cutting planes of the sagittal, coronal and transversal views.

Figure 3. (A) Rationale of the Psychophysiological Interaction Analysis (PPI): The PPI aimed to identify brain regions that were more strongly connected to frontoparietal control areas in the repetition versus sequential condition. (B) and (C) Results of the PPI analysis showing visual areas that were more strongly connected to the right (B, pink color) or left (C, yellow color) Intraparietal Sulcus (IPS) in the repetition versus sequential condition. Crosshair lines show cutting planes of the sagittal, coronal and transversal views.

Figure 1

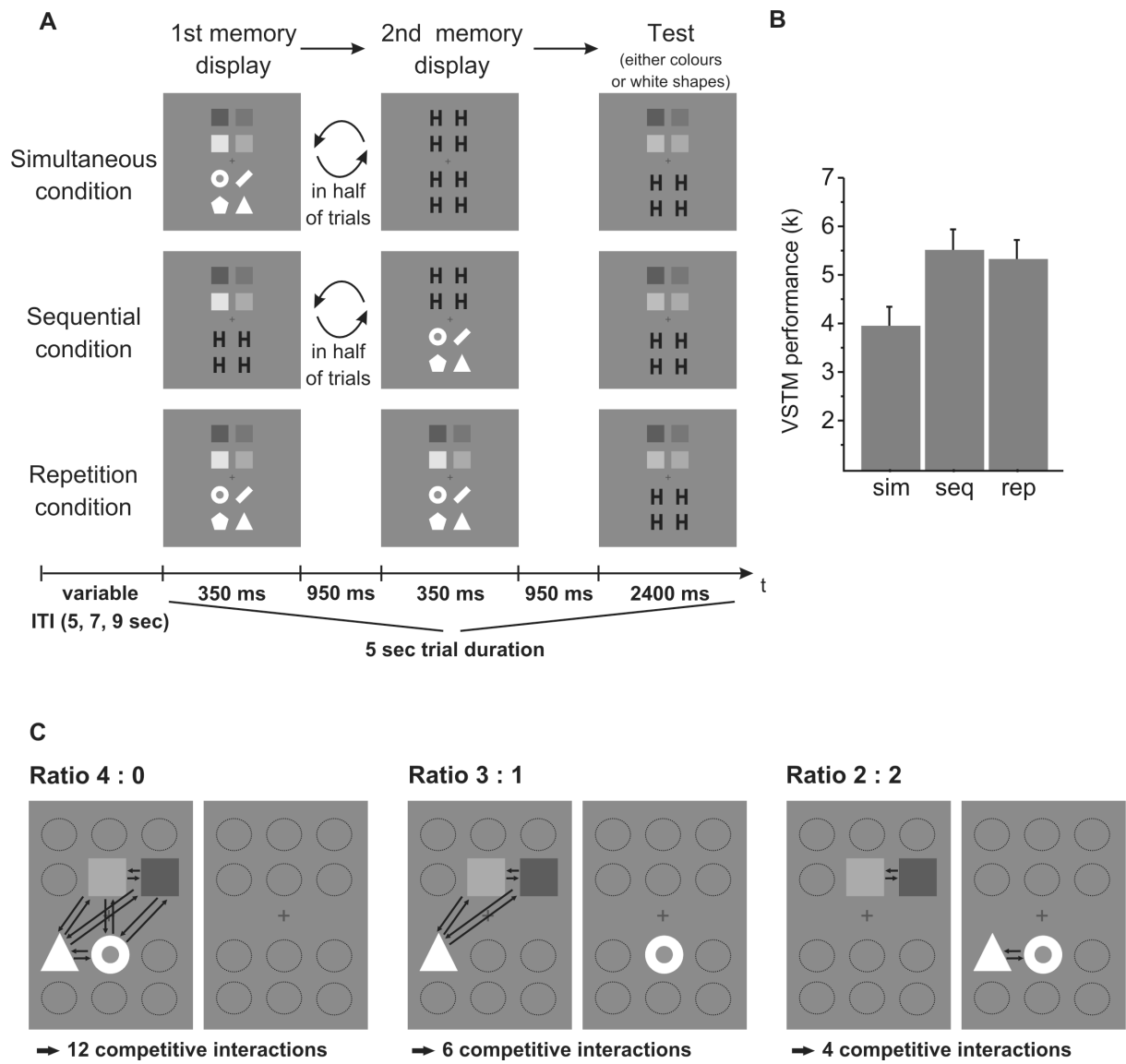


Figure 2

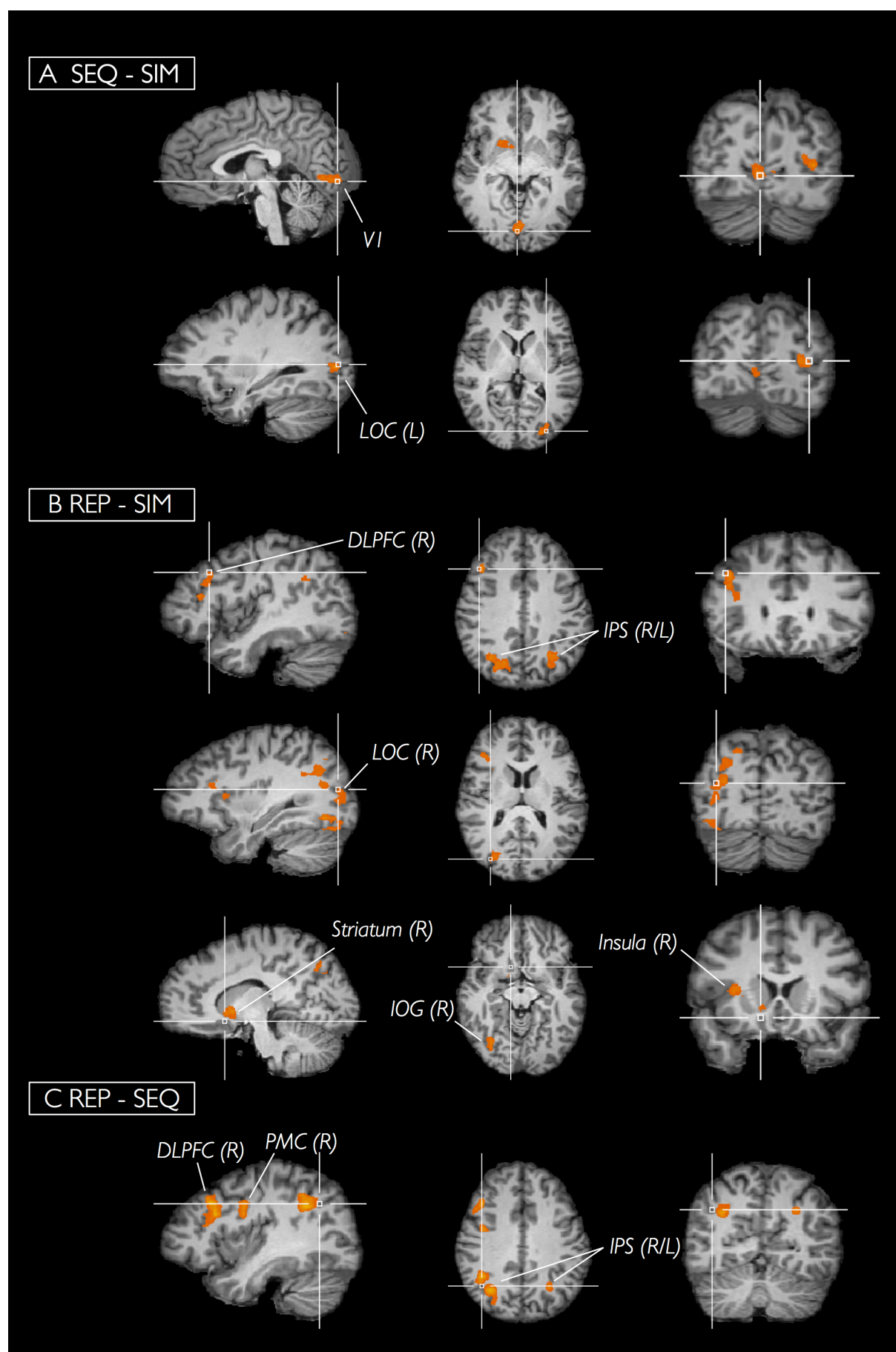


Figure 3